

**THE RESPONSE OF LARVAL GROWTH RATE TO TEMPERATURE
IN THREE SPECIES OF COENAGRIONID DRAGONFLIES
WITH SOME COMMENTS ON *LESTES DISJUNCTUS*
(ODONATA: COENAGRIONIDAE, LESTIDAE)**

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Abstract

Larval growth rate has the same temperature coefficient in three species of coenagrionids, but *Argia vivida* and *Amphiagrion abbreviatum*, which frequently live in geothermally heated water, grow fastest at 29.0-30.0°C compared with 23.4°C for *Coenagrion resolutum*, which lives in cooler water. Survival below 15°C in the laboratory was much better in *C. resolutum*. These characteristics are reflected in the distributions of the three species, *C. resolutum* ranging much further north in North America than the other two species, but not penetrating as far south. By contrast, the temperature coefficient for *Lestes disjunctus* is higher than that of the coenagrionids, and this is related to a different life history. In the coenagrionids, one or more winters are spent in the larval stage. In *L. disjunctus*, winter is spent in the egg stage, and larval growth must be completed quickly.

Introduction

Pritchard et al. (1996) discussed life-history evolution in relation to the invasion of new thermal environments in several groups of aquatic insects. They pointed out that, although different stages of an insect's life cycle usually occupy different niches, evolution in any one stage must be integrated into the whole life cycle. They also pointed out that an alternative to shifts in metabolic responses to temperature is the evolution of life-history phenomena such as diapause. They showed that 56.6% of the between-taxon variation in thermal reaction norms of aquatic insect eggs was associated with differences at the ordinal level, 13.7% at the family level, 7.3% at the generic level, 14.4% at the species level, and 8.0% at the population level, implying that adaptation to new thermal environments for egg development is constrained by phylogenetic inertia. Non-diapausing eggs of Odonata do not vary in thermal reaction norms within the Order, and eggs of all species considered have an optimum development temperature

of 30-35°C. All of these dragonflies oviposit in relatively warm water during summer. This apparent inflexibility of egg development places a premium on interspecific variation in the response of larval development to temperature, if larvae of different species live in different thermal regimes or have different life-history types.

Krishnaraj & Pritchard (1995) compared the effect of temperature on growth rates of larvae of two coexisting damselflies with different life-history types. They showed that *Lestes disjunctus* (Sélys) grew faster than *Coenagrion resolutum* (Hagen in Sélys) at each of the fixed temperatures from 10 to 25°C used in laboratory experiments. *Lestes disjunctus* also had a higher temperature coefficient, and an estimated maximum growth rate at 28.8°C, whereas *C. resolutum* grew fastest at 22.4°C.

In this paper we compare thermal adaptation of larval growth rate in *Coenagrion resolutum*, which lives in cold water, with two coenagrionids that live in geothermally heated habitats. We then examine how thermal adaptation in these coenagrionids compares with *L. disjunctus*, a species with a different type of life history.

Methods

Argia vivida (Hagen in Sélys) and *Amphiagrion abbreviatum* (Sélys) live together in geothermal habitats throughout the overlapping parts of their ranges. Larvae for our experiments were collected during 1994 from two sites in Banff, Alberta (51°10'N, 115°34'W): *A. vivida* from the Cave and Basin Springs at the base of Sulphur Mountain; and *A. abbreviatum* from the Vermilion Spring, 4 km across the Third Vermilion Lake from the Cave and Basin. Further details of these sites are given in Pritchard & Kortello (1997). The data for *C. resolutum*, originally presented by Krishnaraj & Pritchard (1995), represent larvae collected from the Research Pond on the campus of the University of Calgary (51°5'N, 114°7'W) during 1992/1993.

Larvae were placed individually in small plastic containers filled with 75 ml of dechlorinated tap water. We then placed these containers in Styrofoam™ floats in water baths that maintained nominal fixed temperatures between 10°C and 35°C. *Coenagrion resolutum* was reared successfully only at 10-25°C, *A. vivida* at 12.5-30°C, and *A. abbreviatum* at 12.5-32.5°C, although few data were obtained for the warm-water species below 20°C. We read temperatures twice daily, and used actual mean temperatures experienced by each larva between moults in the analysis. Photoperiod was maintained at 16 h light: 8 h dark to simulate early summer conditions and prevent larval diapause.

We fed larvae ad libitum with *Daphnia magna* (Straus). Larvae were checked for moulting every day, and head width of each larva was recorded one day after each moult. Growth rate was calculated from the formula:

$$[1] \quad \%G_n = \frac{L_{n+1} - L_n}{T_n} \cdot \frac{100}{(L_{n+1} + L_n)/2},$$

where

$\%G_n$ = mean percentage growth rate of stadium n (mm mm⁻¹ day⁻¹)
 L_n = head width of stadium n (mm)

L_{n+1} = head width of the next stadium (mm)

T_n = total days spent in stadium n (days).

We assessed the influences on growth rate with a general linear model (Neter et al. 1996) that considered species as a fixed, categorical effect, and size at the beginning of the stadium, temperature, and temperature² as continuous covariates. The analysis initially also considered all interactions between species and the covariates, but non-significant interactions were excluded by backward elimination ($\alpha = 0.05$). Prior to analysis we transformed growth rate to natural logarithms to control heteroscedasticity and normalize residuals. Comparisons of parameter estimates among species involved Šidák's multiplicative inequality to control the experiment-wise Type I error rate to $\alpha = 0.05$ (Sokal & Rohlf 1995).

Analysis of the general linear model provided parameter estimates to the following quadratic equation for each species:

$$[2] \quad \ln \%G = a + b_1 S + b_2 T + b_3 T^2$$

where

- a = intercept
- b_1 = partial regression coefficient for size (head width, S)
- b_2 = partial regression coefficient for temperature (T)
- b_3 = partial regression coefficient for temperature² (T^2).

Given these estimates, the temperature that maximizes growth rate, T^* , can be found by setting the first derivative of equation 2 with respect to temperature equal to 0 and solving for T , yielding:

$$[3] \quad T^* = -b_2/2b_3$$

To illustrate the relation between $\%G_n$ and temperature in isolation from the effects of differences in body size (Fig. 1) we adjusted observed $\%G_n$ as follows. First, we estimated the expected $\%G_n$ for each larva for the temperature it experienced as though it had the average size of all individuals of its species, based on the prediction equation from the general linear model. To this expected value we then added the residual from the general linear model for the larva under consideration.

Results

Percentage growth rate ($\%G_n$) decreased with larval size ($F_{1,342} = 32.40$, $p < 0.001$) for all three species (see Table 1 for partial regression coefficients). However, the strength of this effect differed significantly among the three species ($F_{2,342} = 4.73$, $p < 0.01$). In particular, growth rate declined more quickly with increasing size for *A. vivida* than for *C. resolutum* ($t_{342} = 3.07$, $p < 0.1$), whereas neither species differed significantly from *A. abbreviatum* ($p > 0.05$ in both cases).

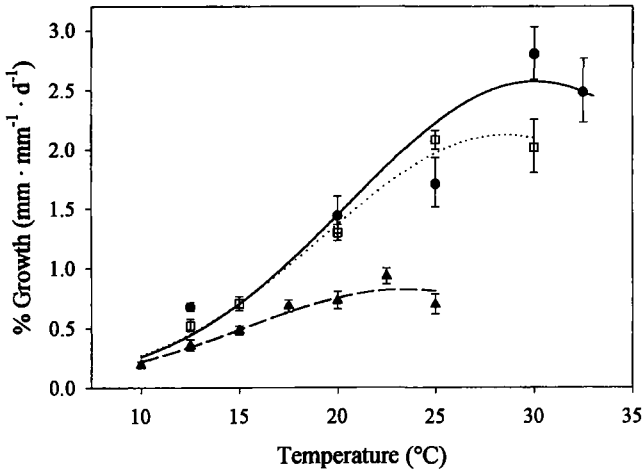


Figure 1. Mean (\pm SE) percent growth rates of *Coenagrion resolutum* (triangles), *Argia vivida* (squares), and *Amphiagrion abbreviatum* (circles) at fixed temperatures. Growth rates are predicted from equation 2 (see text) using average size of experimental animals.

Table 1. Intercepts and partial regression coefficients (\pm SE) for the effects of size and temperature on growth rate for larvae of *Coenagrion resolutum*, *Argia vivida*, and *Amphiagrion abbreviatum* ($p < 0.001$ except ¹ $p < 0.01$ and ² $p < 0.05$).

Effect	<i>C. resolutum</i>	<i>A. vivida</i>	<i>A. abbreviatum</i>
Intercept	-3.7292 ± 0.3843	-2.5583 ± 0.4994	-3.4689 ± 0.5592
Size	-0.1703 ± 0.0626^1	-0.5335 ± 0.1016	-0.2519 ± 0.1176^2
Temperature	0.3366 ± 0.0397	0.3366 ± 0.0397	0.3366 ± 0.0397
Square of Temp.	-0.0072 ± 0.0011	-0.0058 ± 0.0008	-0.0056 ± 0.0009

In general, percentage growth rate increased with increasing temperature (Fig. 1: $F_{1,342} = 68.02$, $p < 0.001$), although growth rate levelled off or even declined slightly near each species' thermal maximum (effect of temperature², $F_{1,342} = 41.01$, $p < 0.001$). The linear effect of temperature did not differ significantly between species ($F_{2,340} = 2.98$, $p > 0.05$); so this interaction term was excluded from the general linear model. In contrast, the quadratic term did differ significantly between species ($F_{2,342} = 8.24$, $p < 0.001$), *A. vivida* and *A. abbreviatum* not differing significantly from each other ($t_{342} = 0.82$, $p > 0.4$), but both species differing from *C. resolutum* ($p < 0.001$ in both cases). Based on the partial regression coefficients (Table 1), growth rate is maximal at the following temperatures for each species: *C. resolutum*, 23.38°C; *A. vivida*, 29.01°C; *A. abbreviatum*, 30.05°C.

Discussion

Larvae of *Argia vivida* and *Amphiagrion abbreviatum*, like *Lestes disjunctus* (Krishnaraj & Pritchard 1995), achieve maximum growth rate at higher temperatures than *Coenagrion resolutum*. However, whereas *L. disjunctus* had a significantly higher partial regression coefficient for temperature than *C. resolutum*, the linear effect of temperature did not differ significantly between the three coenagrionids. The differences between the three species in Fig. 1 reflect the effect of higher temperatures (the temperature² term) and the different coefficients for the size effect.

Norling (1975) classified temperate-zone odonate life histories into two groups. One group, exemplified by the family Lestidae, included obligatory univoltine life histories in which individuals overwinter in a well defined diapausing stage, commonly as eggs. This life-history type requires rapid larval development. The second life-history type is exemplified by the family Coenagrionidae. Individuals usually overwinter in a wide range of larval stadia, larval growth is slower than in lestids, and the life history often extends beyond one year.

The life history of *A. abbreviatum* has not been studied in detail, but larval collections from Vermilion Spring suggest that it is similar to that of *A. vivida*, which spends one or more winters in the larval stage depending on water temperature (Pritchard 1989), as does *C. resolutum* (Baker & Clifford 1981). Thus, the temperature coefficient for larval growth appears related to life-history type rather than to habitat temperature. However, some adaptation to environmental temperatures has clearly occurred at the species level, as the temperature range that is favourable for growth in *A. abbreviatum* and *A. vivida* is shifted upward compared with *C. resolutum*. Consequently, *C. resolutum* is found much further north than the other two coenagrionids. In particular, *C. resolutum* ranges north of 68°N (Cannings & Cannings 1997), whereas *A. abbreviatum* and *A. vivida* go no further north than 52°N, where they occupy geothermally heated water and are not found in streams that freeze in winter. In contrast, at the southern end of its range, *C. resolutum* occurs only in the mountains in Nevada and California (Cannings & Cannings 1997), whereas *A. abbreviatum* and *A. vivida* occur at all elevations and into Baja California.

Whereas the coenagrionids spend the winter in the larval stage, *L. disjunctus* overwinters in the egg stage (Sawchyn & Gillott 1974; Baker & Clifford 1981; Krishnaraj & Pritchard 1995) and so must complete larval development during the growing season in which eggs hatch. The response of growth rate to temperature in *L. disjunctus* allows it to achieve this high rate of growth in most habitats in which *C. resolutum* occurs, ranging almost as far north (Cannings & Cannings 1997) and being restricted to the mountains in the southern part of its range (Walker 1953). In spite of having a maximal growth rate at temperatures comparable with those of the warm-water coenagrionids, *L. disjunctus* has not been recorded from geothermal habitats. Presumably this is because such permanent habitats do not provide appropriate conditions for overwintering eggs.

Finally, this study raises the possibility that phylogenetic constraint is not the explanation for the relatively invariant thermal reaction norm of dragonfly eggs (Pritchard et al. 1996). Instead, the flexibility of larval development may create an

evolutionary line of least resistance, relaxing evolutionary pressure on the egg stage. Distinguishing between the two alternatives will not be easy, but they do emphasize the fact that insect life histories are integrated units and need to be treated as such in evolutionary as well as ecological studies.

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